THE DISTRIBUTION AND PATTERNS OF SPECIES DIVERSITY OF LAND SNAILS IN EASTERN AUSTRALIA

JOHN STANISIC

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For coastal and near-coastal eastern Australia (Torres Strait islands to the New South Wales-Victorian border), it is predicted that the total number of species of land snails will exceed 700 (presently less than 400 are known) when taxonomic revisions are completed. Most of this snail diversity is concentrated in a coastal strip less than 200km wide. Species diversity and endemicity is greatest for rainforest. The climate induced attrition of mesic communities since the Miocene (more pronounced in the Pleistocene), their survival within refugia and their subsequent radiation and dispersal under more favourable conditions, are fundamental to explaining how these diversity patterns arose. Endemicity and species diversity of land snails in eastern Australia is also high on limestone outcrops. In an extraordinary situation in the Macleay Valley, northeastern New South Wales, rainforest and limestone are juxtaposed, resulting in diversity levels which are exceptionally high on a world scale.

Species composition within areas of high snail diversity indicates that these snail communities evolved through a long term accumulation of taxa rather than localised radiations In a few cases, e.g. isolated dry vine thickets, between-site diversity is increased by geographic replacement of taxa.

Today the distribution of land snails in eastern Australia strongly reflects rainforest biogeography; furthermore land snail community structure correlates with rainforest structural types. This suggests that land snails can have strong predictive value in identifying climatic refugia. ☐*Land snails, Mollusca, eastern Australia, biodiversity, communities, limestone, rainforest, distribution*

John Stanisic, Queensland Museum, PO Box 3300, South Brisbane, Queensland, 4101, Australia; *21 November 1993.*

The study of land snail diversity in eastern Australia is in its infancy. Faunal checklists and species' descriptions have not been complemented by 'follow-up' survey work and revisionary studies. The works of Cox (1868) and Iredale (1937a, 1937b, 1938) still form the basis of terrestrial malacological knowledge for this region. Contemporary contributions of Smith & Kershaw (1979, 1981) focused on Victorian and Tasmanian species and more recently Smith (1992) produced a revised checklist of all Australian land snails. Attempts at 'modern' biogeographic syntheses are limited to McMichael & Iredale (1959), Solem (1959), Bishop (1981) and Smith (1984). With the exception of some rainforest surveys of the mid-1970's (e.g. Broadbent & Clark, 1976) and a survey of the New England district, New South Wales (Simpson & Stanisic, 1986), there has been a lack of comprehensive field work directed at recording and documenting the east-coast land snail fauna.

For the past thirteen years the Queensland Museum Malacology Section has been engaged in a systematic collection programme extending from the Torres Strait islands to the New South Wales/Victorian border in an effort to redress these shortcomings. More than 1000 sites (a site is an area $<1km^2$ in size) (Fig. 1) have been sampled by hand-collecting live and dead specimens and sorting retrieved leaf litter (land snails usually possess a hard shell, which remains in the litter after death and allows for post-mortem sampling). Results indicate that the diversity of the east-coast land snail fauna has been grossly underestimated. While a great deal of taxonomic work needs to be completed before a comprehensive biogeographic synthesis can be presented, preliminary findings make it possible to promote these often-neglected animals in the biodiversity debate. This paper examines some aspects of land snail diversity in eastern Australia which have come to light during the course of the study.

The major physiographic features of the study area are the Great Dividing Range and a series of coastal ranges which rise from a narrow coastal plain to provide barriers to onshore, rain-bearing winds. Consequently, in addition to drier sclerophyll vegetation, these mountains support rainforest that varies in structure and extent from north to south (Webb & Tracey, 1981) and from sea level to mountain summit. In more westerly areas, rainforest in the form of dry vine thickets occurs sporadically on volcanic soils and rock outcrops, in particular limestone. Field work has been focused on censusing the snail communities within these habitats, which occur mainly in a narrow coastal strip less than 200km wide.

The following abbreviations have been used in the text: NSW, New South Wales; NEQ, northeastern Queensland; MEQ, mideastern Queensland; SEQ, southeastern Queensland.

LAND SNAILS AND RAINFOREST

The association between land snails and moist, closed forests is an ancient one. Land snails make their first appearance in the fossil record in the Upper Carboniferous coal beds of Europe and North America and it has been suggested (Solem & Yochelson, 1979) their early radiation was closely tied to the appearance and proliferation of angiosperms. The basis for the association is ecological. Those factors which favour rainforests (high nutrient soils, moisture) are also those which favour land snails. Rainforests provide the additional benefit of shelter. In eastern Australia this bond has been more strongly reinforced by climatic and geologic events which shaped present-day, east-coast physiography.

Rainforest was once more widespread in Australia than today (Martin, 1981). With the onset of arid episodes in the Miocene (Galloway & Kemp, 1981), rainforest either disappeared or was restricted in distribution in many areas (Fig. 2). In the east, uplift of the Great Divide and volcanic activity combined to provide favourable moisture-soil conditions which ameliorated the effects of continental drying and allowed mesic communities to persist. Subsequently rainforest has fluctuated greatly in extent (Kershaw, 1980, 1981) and the extreme drying events of the Quaternary would have seen rainforest retreat to refugia such as moist uplands and gully heads, emerging only in wetter periods (Webb & Tracey, 1981). The animal communities within them, in particular the strongly moisture-dependent, soft-bodied land snails, would have been placed under considerable stress. In some cases extinctions would have occurred.

FIG 1. Distribution of land snail collecting sites in eastern Australia, Queensland Museum 1980-1993 (Ca, Cairns; Ma, Mackay; Ro, Rockhampton; Br, Brisbane; Sy, Sydney).

The fact that most land snails in eastern Australia (over 90%) now occur in rainforest indicates just how critical the persistence of moist refugia was to their survival in this region.

Within the rainforest vegetation mosaic, snail diversity and community composition differ markedly with latitude and from site to site. The regions which have the greatest number of

FAMILY	Named species[+]	Estimated new species*
Hydrocenidae	4	5
Helicinidae	5	3
Cyclophoridae	2	2
Pupinidae	19	10
Diplommatinidae	4	3
Achatinellidae	3	0
Pupillidae	20	4
Enidae	1	1
Megaspiridae	1	1
Succineidae	3	1
Subulinidae	1	0
Rhytididae	27	8
Caryodidae	9	0
Helicodiscidae	1	0
Punctidae	13	7
Charopidae	74	200
Athoracophoridae	1	3
Cystopeltidae	4	2
Helicarionidae	46	40
Camaenidae	105	35
Corillidae	1	0
Rathouisiidae	2	0
TOTAL	347	325

TABLE 1. Faunal composition of eastern Australian land snail diversity ([+]based on various sources; *based on undescribed species identified in the collections of the Queensland Museum).

species are those with dissected topography (steep gorges and high mountains) that support diverse rainforest vegetation communities (e.g. Wet Tropics, Border Ranges). Moisture stability and the availability of diverse niches have provided an ideal environment for the evolution and persistence of complex snail communities.

LIMESTONE

Limestone outcrops (Fig. 2), in particular large tower karsts such as those present in the Chillagoe-Palmerville region, NEQ, north of Rockhampton, MEQ, and Jenolan, NSW, are significant secondary habitats for land snails. They support remnants of wet-adapted vegetation in otherwise dry, sclerophyll-dominated countryside. Moisture is trapped in crevices and the rock provides a protective niche from wildfires so that in many instances snail communities, quite distinct from those in the surrounding forest, have developed and been maintained. Land snails which inhabit these special refugia also benefit from an ample supply of calcium. Endemicity and specialisation in these limestone snail communities indicate long-term isolation (Stanisic, 1990). In an exceptional case in the Macleay Valley, NENSW, subtropical/warm temperate rainforest and limestone are juxtaposed resulting in extraordinarily high land snail diversity.

FAUNAL COMPOSITION

There are 22 families represented in the east-coast native land snail fauna comprising more than 670 species of which about half are undescribed (Table 1). This compares with estimates of a total Australian fauna of 504 species in 25 families (Smith, 1992) and illustrates the enormous diversity (mostly undescribed) of the east-coast fauna. It is probable that final species numbers for this region will exceed 700. The main contributors to this biodiversity are the Charopidae, Camaenidae and Helicarionidae. The Helicarionidae and Charopidae have their greatest expression in eastern Australia but the Camaenidae are more diverse in other areas of Australia (see Solem, 1992, for overview). The Australian operculate land snails (Hydrocenidae, Helicinidae, Cyclophoridae, Pupinidae and Diplommatinidae) are also largely confined to the east-coast rainforests. The stable moisture regime and volcanically derived acidic soils have provided an ideal environment for slug evolution and three families of slug taxa are represented — the Rathouisiidae, Cystopeltidae and Athoracophoridae. The first is an obligate rainforest group while the latter two have representatives in transitional wet sclerophyll forest as well as closed forests. Semi-slugs, belonging to the family Helicarionidae, display an even greater diversity here with over 30 species present, some restricted to mountain tops. The great majority of these are rainforest dwellers with only a few species occurring in drier sclerophyll forests.

Dry-adapted groups such as the Pupillidae and Punctidae have several representatives in the warm to hot humid forests but are more diverse in the drier vine thickets and forests, and sclerophyll forest.

SITE DIVERSITY

Land snail diversity levels at individual collecting sites have been found to be highly variable and range from about 5 species per site in dry sclerophyll forests to over 40 species per site in some rainforest patches (Fig. 3). Greatest diversity has been recorded in the subtropical rainforests of southeastern Queensland. Binna Burra (Border Ranges) and Booloumba Creek (Conondale Ranges) have yielded in excess of 40 species. From this subtropical zenith diversity diminishes both to the north (tropical forest) and to the south (temperate forests). In most cases increased distance from the coast correlates with a marked drop in diversity so that subcoastal rainforest patches (= dry vine thickets) average about 10 species. Exceptions occur in isolated moist refugia such as those at Carnarvon Gorge, MEQ, and Mt Kaputar (Nandewar Range), NSW, and on limestone outcrops. Hence at Chillagoe, NEQ, more than 25 species have been recorded on limestone in otherwise snail depauperate countryside. In southern NSW limestone outcrops located in areas of sclerophyll woodland (e.g. Abercrombie, Yarrangobilly, Wombeyan, Jenolan) also record above average site diversity levels indicating the probability of highly localised endemism. In NENSW average rainforest site diversity levels are generally 10-20 species but in the Macleay River valley, where limestone occurs within rainforest, species numbers at some sites (Yessabah, 36; Mt Sebastopol, 26) are much higher owing to the presence of limestone endemics (Stanisic, 1990). There are few areas of the world where site diversity levels exceed 30 species (Solem, 1984). In this context eastern Australia is an area of exceptional land snail diversity.

MOSAIC DIVERSITY

Dissected topography associated with the Great Escarpment (Ollier, 1982) and severe palaeoclimatic regimes have combined to produce a diverse pattern of vegetation communities in eastern Australia that support equally diverse land snail assemblages. The result is relatively high diversity within comparatively small areas even though diversity at individual sites is not high.

Mt Bellenden Ker is the second highest mountain (alt. = 1560m) in the Wet Tropics, NEQ. The eastern face is covered in rainforest which is altitudinally stratified into a number of structural

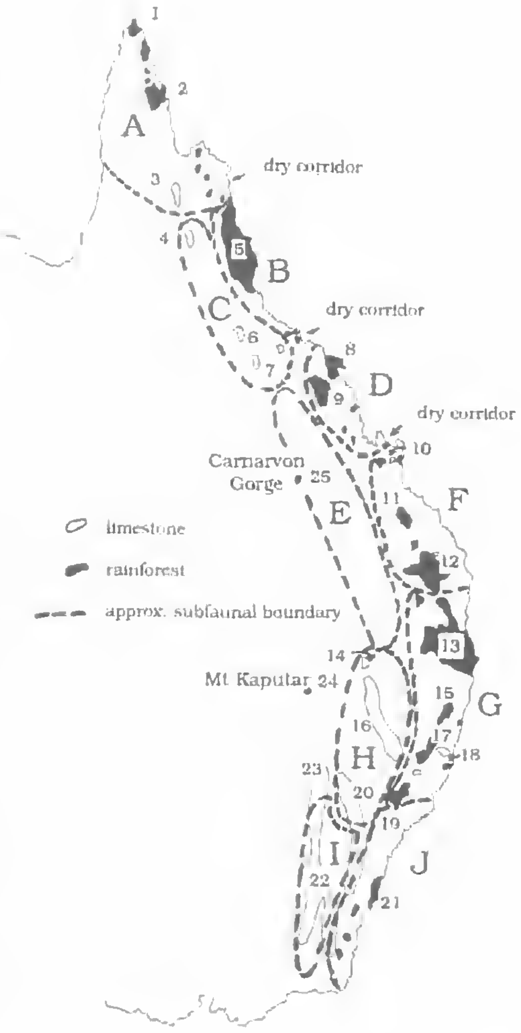


FIG. 2. Distribution of major coastal rainforest blocks and areas of limestone outcrop in eastern Australia. Dotted lines signify possible boundaries for division of land snails into subfaunal units (A-J). 1, Lockerbie Scrub; 2, Iron Range; 3, Palmerville; 4, Chillagoe; 5, Wet Tropics; 6, Greenvale; 7, Broken River; 8, Conway Range; 9, Eungella; 10, The Caves; 11, Bulburin; 12, Gympie; 13, Border Ranges; 14, Ashford; 15, Dorrigo; 16, Manilla- Tamworth; 17, Carrai-Werrikimbe; 18, Macleay Valley; 19, Barrington Tops; 20, Hill End-Captains Flat; 21, Illawarra; 22, Cowra-Yass; 23, Molong. A, Cape York; B, Wet Tropics; C, Einasleigh Uplands; D, mideastern Queensland; E, Brigalow Lands; F, southeastern Queensland; G, Border Ranges-northeastern NSW, H, New England Tablelands; I, Southern Tablelands; J, south coastal New South Wales.

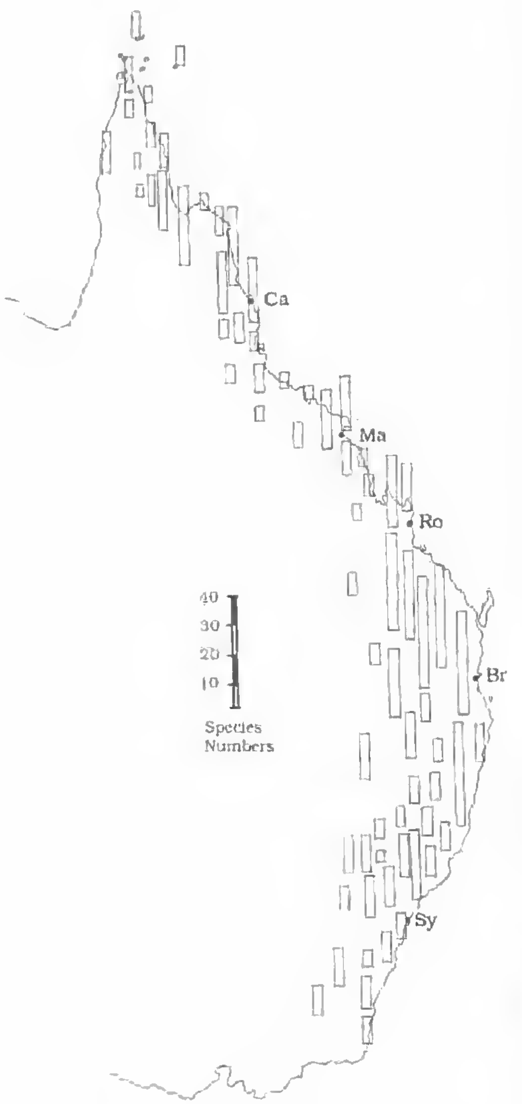


FIG. 3.Comparison of land snail diversity levels at selected sites in eastern Australia (Ca, Cairns; Ma, Mackay; Ro, Rockhampton; Br, Brisbane; Sy, Sydney).

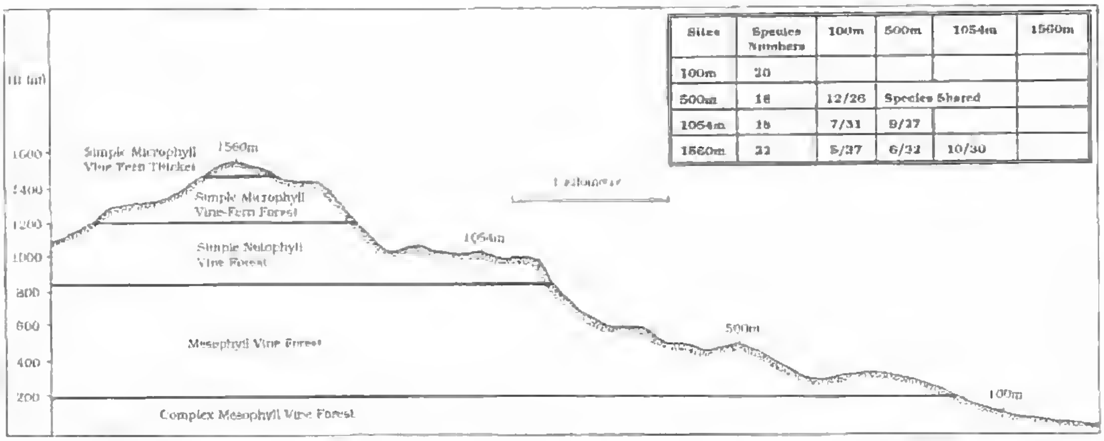
types varying from complex mesophyll vine forest in the lowlands to simple microphyll vine fern forest and thicket near the summit (Fig. 4). Sampling at selected altitudes produced 45 species over all sites. However, few species were present at all altitudes (Fig. 3). Greatest disparity occurred between the base (100m) and the summit (1560m) sites which had only 5 of 37 species in common. This pattern of altitudinal stratification is most marked in the Wet Tropics but is also present at other east-coast localities.

The usual patterns of land snail distribution, which strongly reflect the rainforest/woodland vegetation mosaic are complicated by the presence of limestone (Fig. 2). A large number of outcrops occur along the Great Divide in NSW but those in the Macleay Valley, NENSW, are perhaps the most significant. They are situated in the midst of temperate and subtropical rainforest and even the most easterly outlier (Yessabah) is vegetated by rainforest in spite of being surrounded by much drier countryside (Floyd, 1983). Fifty sites (Fig. 5) were sampled in a area bounded by the Hastings River (south), Nambucca River (north) and the Great Divide (west). Rainforest sites (those without limestone) yielded comparatively low numbers of species (mean 5.64 species/site) but limestone sites were far richer (31.00 species/site). In contrast eucalypt forest sites were relatively snail poor (mean 3.00 species/site). The high diversity found on the limestones results from a combination of widespread species found in surrounding rainforest and eucalypt woodland, and a significant number of limestone endemics (see Stanisic, 1990, for some examples). Some species are confined to individual outcrops. Total diversity was approximately 85 species in the sampled area and was composed of a number of quite distinctive assemblages which have developed under different micro-environments.

In the vine thickets west of Townsville to Sarina, NEQ, there is evidence of geographical replacement of species between widely separate rainforest patches. Individual patches have low species numbers (5-10 species) but diversity over the totality of patches exceeds this because of allopatric speciation. Solem (1984) reported a similar phenomenon in northwestern Australia.

REGIONAL DIVERSITY

Iredale (1937a) first applied the concept of regional diversity to Australian land snails. Although this scheme has received some support (McMichael & Iredale, 1959; Smith, 1984) there has been criticism of its predictive value (Bishop, 1981). Horton (1973) suggested that any zoogeographic subdivision of Australia should consider isolating barriers as well as the climate and vegetation of an area. The proposed methodology (based on bird distribution) has particular relevance to land snails in eastern Australia where their evolution has been driven



Sites	Species Numbers	100m	500m	1054m	1560m
100m	20				
500m	18	12/26	Species Shared		
1054m	18	7/31	9/27		
1560m	22	5/37	6/32	10/30	

FIG. 4. Altitudinal stratification of land snail communities on Mt Bellenden Ker, NEQ (12/26 means that a total of 26 species were collected at 100m/500m sites and 12 were common to both).

by climate-based changes to mesic vegetation communities since the Miocene. A full outline of a scheme of land snail subfaunal units in eastern Australia will be presented elsewhere but the approximate boundaries of the units are shown in Figure 2. The proposed scheme divides the eastern Australian land snails into a number of smaller subregional units ('subfaunas') defined by a coincidence of species ranges and separated by species range endpoints (faunal breaks). These faunal breaks express past and present environmental discontinuities and may coincide with present climatic barriers (dry corridors) or, less obviously, reflect a more complex history of environmental sifting. Initial investigations indicate that the proposed land snail subfaunas in Queensland show considerable concordance with the natural biogeographic regions outlined by Stanton & Morgan (1977) which were defined by climate, vegetation and landform.

COMMUNITY STRUCTURE

The species composition of land snail communities present at any site usually consists of narrow range endemics and species which have a more widespread distribution. The proportion of narrow range endemics is greatest in refugia (moist uplands, limestone outcrops) whereas widespread species tend to dominate drier vine thickets and eucalypt woodland. These land snail communities appear to be a result of an accumulation of species rather than localised radiations. In only a few cases can minor local radiations be identified, however, the wider picture is one of an ancient southern element complemented by a colonising northern element. The southern element has more relicts in the north (most notably among the Charopidae) than vice versa. Charopids are numerically dominant in many places especially in areas of high diversity where site numbers can range 8-12 species. Sites with large numbers of charopids (whether in the north or south) or with any narrow endemic land snails are significant (Stanisic, 1990) because they indicate long-term moisture stability.

DISTRIBUTION PATTERNS

Solem (1984) predicted that the median linear range for all land snail species would be considerably less than 100km (and probably less than 50km). Stanisic (1990) showed that a number of eastern Australian Charopidae had much more extensive ranges (150-200km). Most east-coast rainforest land snails show considerable breadth of distribution within major rainforest tracts (Wet Tropics; mideastern Queensland; araucarian vine forests of southeastern Queensland; Border Ranges etc.). Upland refugia and limestone outcrops have the greatest number of narrow range endemics. In drier vine thickets species can range over considerable distance but occur sporadically in isolated and scattered thickets. Species which live in eucalypt woodland tend to have the widest ranges. These features highlight the importance of refugia for land snail survival, the significance of the rainforest ecosystem in providing long-term moisture stability and the broad environmental adaptability of dry-adapted forms.

While it is possible to comment informatively on local species richness, discussion of species abundance (numbers of individuals) remains largely qualitative and speculative. No formal study of land snail abundance (in time and space) has yet been attempted in eastern Australia.

Limestone sites and the araucarian vine forests of southeastern Queensland have the greatest numbers of species living sympatrically. However, because land snails have fairly specific microhabitat requirements the local abundance of a particular species will vary greatly depending on the degree of environmental heterogeneity (microhabitat diversity). Hence in MEQ large camaenids are dominant overall but reach greatest numbers in rocky talus slopes. On limestone outcrops the density of individuals is enhanced by the presence of sheltered southeasterly aspects along driplines. Many of the environments with high snail numbers are seasonally dry and fluctuations in local abundance may occur but this has not yet been not quantified. In the Wet Tropics large camaenids do not appear to have the same local abundance as those which occur in MEQ so that locating large numbers of individuals is difficult. Similar situations have been encountered in the wetter forests of NENSW and SEQ. Reasons for this are not obvious. Solem (1984) suggested that there might be advantages

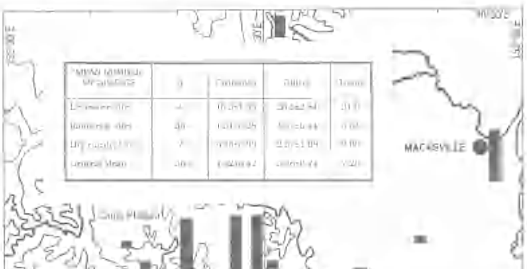


FIG. 5.The influence of limestone (four highest peaks in centre) on land snail site diversity levels in the Macleay Valley, NENSW (not all sites shown; rainforest sites are those without limestone).

to the limited activity periods of land snails in drier environments. The effects of competitive interaction between and among species is unknown as are the effects of densities on population. There is a desperate need for basic ecological studies of eastern Australian land snails with particular emphasis on the aspect of abundance.

CONSERVATION

As indicators of climatic refugia land snails appear to be a potentially significant group of organisms in the biodiversity/conservation debate. In spite of the large numbers of undescribed species, land snails represent a manageable taxonomic unit for use in land management decisions. Today their distributions reflect rainforest biogeography and in many instances land snail community composition correlates strongly with rainforest structural types. This suggests that land snails can have strong predictive value in identifying potential reservation areas.

ACKNOWLEDGEMENTS

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LITERATURE CITED

BISHOP, M.J. 1981. The biogeography and evolution of Australian land snails. Pp. 924-954. In Keast, A. (ed.), 'Ecological biogeography of Australia'. (W. Junk: The Hague).

BROADBENT, J. & CLARK, S. 1976. 'A faunal survey of east Australian rainforests: interim report'. (Australian Museum: Sydney).

COX, J.C. 1868. 'A monograph of Australian land shells'. (W. Maddock: Sydney).

FLOYD, A.G. 1983. 'Rainforest vegetation of the Yessabah limestone belt and Carrai Plateau'. (Unpublished Internal Report, New South Wales National Parks and Wildlife Service, Sydney).

GALLOWAY, R.W. & KEMP, E.M. 1981. Late Cainozoic environments in Australia. Pp. 52-80.

In Keast, A. (ed.), 'Ecological biogeography of Australia'. (W. Junk: The Hague).

HORTON, D. 1973. The concept of zoogeographic subregions. Systematic Zoology 22: 191-195.

IREDALE, T. 1937a. A basic list of the land Mollusca of Australia. Australian Zoologist 8: 287-333.

1937b. A basic list of the land Mollusca of Australia. Part II. Australian Zoologist 9: 1-39.

1938. A basic list of the land Mollusca of Australia. Part III. Australian Zoologist 9: 83-124.

KERSHAW, A.P. 1980. Long term changes in north-east Queensland rainforest. Pp. 32-38. In Wright, J., Mitchell, N. & Watling, P. (eds), 'Reef, rainforest, mangroves, man'. (Wildlife Preservation Society of Queensland: Brisbane).

1981. Quaternary vegetation and environments. Pp. 81-101. In Keast, A. (ed), 'Ecological biogeography of Australia'. (W. Junk: The Hague).

McMICHAEL, D.F. & IREDALE, T. 1959. The land and freshwater Mollusca of Australia. Pp. 224-245. In Keast, A., Crocker, R.L. & Christian, C.S. (eds), 'Biogeography and ecology in Australia'. (W. Junk: The Hague).

MARTIN, H.A. 1981. The Tertiary flora. Pp. 391-406. In Keast, A. (ed.), 'Ecological biogeography of Australia'. (W. Junk: The Hague).

OLLIER, C.D. 1982. The Great Escarpment of eastern Australia: tectonic and geomorphic significance. Journal of the Geological Society of Australia 29: 13-23.

SIMPSON, R.D. & STANISIC, J. 1986. Faunal survey of New England. II. The distribution of gastropod molluscs. Memoirs of the Queensland Museum 22: 115-139.

SMITH, B.J. 1984. Regional endemism of the south-eastern Australian land mollusc fauna. Pp. 178-188. In Solem, A. & Van Bruggen, A.C. (eds), 'World-wide snails. Biogeographical studies on non-marine Mollusca'. (E.J. Brill/Dr W. Backhuys: Leiden).

1992. Non-marine Mollusca. Pp. 1-405. In Houston, W.W.K. (ed.), 'Zoological Catalogue of Australia, Vol. 8'. (Australian Government Printing Service: Canberra).

SMITH, B.J. & KERSHAW, R.C. 1979. 'Field guide to the non-marine molluscs of southeastern Australia'. (ANU Press: Canberra).

1981. 'Tasmanian land and freshwater molluscs. Fauna of Tasmania handbook No.5'. (University of Tasmania: Hobart).

SOLEM, A. 1959. Zoogeography of the land and freshwater Mollusca of the New Hebrides. Fieldiana: Zoology 43: 239-359.

1984. A world model of land snail diversity and abundance. Pp. 6-22. In Solem, A. & Van Bruggen, A.C. (eds), 'World-wide snails. Biogeographical studies on non-marine Mollusca'. (E.J. Brill/Dr W. Backhuys: Leiden).

1992. Camaenid land snails from southern and eastern South Australia excluding Kangaroo Island. Records of the South Australian Museum, Monograph Series 2: 1-338.

SOLEM, A. & YOCHELSON, E.L. 1979. North American Palaeozoic land snails, with a summary of other Palaeozoic non marine snails. United States Geological Survey, Professional Paper 1072: 1-42.

STANISIC, J. 1990. Systematics and biogeography of eastern Australian Charopidae (Mollusca, Pulmonata) from subtropical rainforests. Memoirs of the Queensland Museum 30: 1-241.

STANTON, J.P. & MORGAN, G. 1977. The rapid selection and appraisal of key and endangered sites: the Queensland case study. University of New England School of Natural Resources, Report No. PR4, 17pp.+14appendices.

WEBB, L.J. & TRACEY, J.G. 1981. Rainforests: patterns and change. Pp. 606-694. In Keast, A. (ed.), 'Ecological biogeography of Australia'. (W. Junk: The Hague).